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PERSISTENCE AND EXTINCTION IN CONTINUOUS AGE-STRUCTURED POPULATION MODELS

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Abstract—Survival analyses of populations are developed in a continuous process. Persistence and extinction criteria of a class of continuous age-structured population models with separable mortality function and fertility function are established by investigation of asymptotic behaviors of solutions of McKendrick–von Foerster equation.

1. INTRODUCTION

The question of persistence and extinction of populations is of importance in ecology. Since the start of the Cambrian 10^8–10^9 years ago there have been 10^8–10^9 species extinctions [1]. Many existent species still face the risk of extinction because of increase of pollutants, by-products of the development of modern science and technology, in the environment.

While there are many studies of persistence in continuous community models [2–6], there are few explicitly on one species. Recently, Hallam and Ma [7, 8] studied survival in populations with demographic variations, but the age structure is ignored.

In this paper, we consider certain special continuous population models with age structure. The existence and uniqueness of the solution are established first. By using a transformation and a comparison technique, some basic results for persistence and extinction are presented.

The age-structured continuous population model that we discuss in this paper is the so-called McKendrick [9] equation or von Foerster [10] equation

$$\frac{\partial \rho(a,t)}{\partial a} + \frac{\partial \rho(a,t)}{\partial t} = D(a,t,P)\rho(a,t), \tag{1}$$

$$\rho(0,t) = \int_0^\infty n(a,t,P)\rho(a,t)\,da, \tag{2}$$

$$\rho(a,0) = \phi(a), \tag{3}$$

where $\rho(a,t)$ is the density distribution of a population so that

$$\int_\alpha^\gamma \rho(a,t)\,da$$

gives the number of individuals with age between α and γ at time t; $D(a,t,P)$ is the age specific mortality function; $n(a,t,P)$ is the age specific fertility function;

$$P(t) = \int_0^\infty \rho(a,t)\,da$$

is the total population size; and $\phi(a)$ is the initial age distribution.

This is a first order hyperbolic partial differential equation and it can be solved theoretically by using the method of characteristics. However, when this method is applied, the unknown function is still involved implicitly in the expression for the solution. Hence, the solution is not explicitly found, and, in general, the analytic study of the model is very difficult, especially, when time variation in demographic parameters and density dependence are included in the formulation.

In order to obtain certain theoretical results several studies have assumed that the mortality function μ and the fertility function β are time independent or density independent (e.g. Refs [11–23]). Clearly, when food limitations and environmental effects are considered, it is more realistic to assume that the mortality and the fertility are time dependent and density dependent.

Swick [24] studied persistence and extinction under the assumptions that $\mathbf{D}(a) \leqslant D(a, t, P) \leqslant \bar{D}(a)$, $\mathbf{n}(a)P^r \leqslant n(a, t, P)$ or $n(a, t, P) \leqslant \bar{n}(a)P^r$. The persistence and extinction results are determined by $\mathbf{n}(a)$, $\bar{n}(a)$, $\mathbf{D}(a)$ and $\bar{D}(a)$. Hence, in fact, time variation is ignored. Haimovici [25] studied dynamics of populations involving resources and pollution, but persistence and extinction of populations were not considered.

Here, we assume that the population is subjected to a fluctuating environment so that the mortality function and the fertility function are time varying, and that a limited food supply only affects the mortality representation. Furthermore, we assume that the mortality function is separable in the variables a, t and P. These assumptions, together with some others, are collected as follows.

$$D = c(t) + \mu(a) + f(P(t)), \tag{4}$$

where

$c(t)$ = an exogenous factor that increases the death rate of the population [7] and satisfies

$$0 \leqslant c(t) \leqslant \bar{c} < \infty; \tag{5}$$

$\mu(a)$ = the age dependent factor, such that

$$0 < \mu(a) \leqslant \bar{\mu} < \infty; \tag{6}$$

$f(P)$ = the density function which satisfies $f(0) = 0$, and

$$f(P) \leqslant \bar{f} < \infty, \quad 0 < f'(P) \leqslant k, \quad \forall P \geqslant 0.$$

The fertility function is assumed to be of the separable form

$$n = b(t)\beta(a),$$

where $0 < b_* \leqslant b(t) \leqslant b^*$, and $\beta(a) \geqslant 0$ has compact support on $[0, \infty)$ because no individuals would survive beyond some maximum age; that is, $\exists A > 0$, such that $\beta(a) = 0$, $\forall a \geqslant A$. Denote

$$\sup_{0 \leqslant a \leqslant A} \beta(a)$$

by $\bar{\beta}$.

To have solutions which are continuous, we also assume that

$$\phi(0) = b(0) \int_0^\infty \beta(a)\phi(a)\,da. \tag{7}$$

2. EXISTENCE AND UNIQUENESS OF SOLUTIONS

In this section, we will use the method in Gurtin and MacCamy [12] to show existence and uniqueness.

By employing the characteristics curves, it is easy to get the solution representation

$$\rho(a, t) = \begin{cases} \phi(a - t)\exp\left[-\int_0^t (c(\tau) + \mu(a - t + \tau) + f(P(\tau)))\,d\tau \right], & a \geqslant t \\ B(t - a)\exp\left[-\int_0^a (c(t - a + \tau) + \mu(\tau) + f(P(t - a + \tau)))\,d\tau \right], & a < t \end{cases} \tag{8}$$

where

$$B(t) = \rho(0, t) \tag{9}$$

is the birth rate. Substituting equations (8) into (2) and changing several variables of integration yields

$$B(t) = \int_0^t b(t)\beta(t - a)\exp\left[-\int_0^{t-a} (c(a + \tau) + \mu(\tau) + f(P(a + \tau)))\,d\tau \right] B(a)\,da$$

$$+\int_0^\infty b(t)\beta(a+t)\phi(a)\exp\left[-\int_0^t (c(\tau)+\mu(a+\tau)+f(P(\tau)))\,d\tau\right]da \tag{10}$$

and

$$P(t)=\int_0^t B(a)\exp\left[-\int_0^{t-a}(c(a+\tau)+\mu(\tau)+f(P(a+\tau)))\,d\tau\right]da$$

$$+\int_0^\infty \phi(a)\exp\left[-\int_0^t (c(\tau)+\mu(a+\tau)+f(P(\tau)))\,d\tau\right]da. \tag{11}$$

Let

$$K(a,t,P)=\exp\left[-\int_0^{t-a}(c(a+\tau)+\mu(\tau)+f(P(a+\tau)))\,d\tau\right], \tag{12}$$

$$M(a,t,P)=\exp\left[-\int_0^t (c(\tau)+\mu(a+\tau)+f(P(\tau)))\,d\tau\right]. \tag{13}$$

Then

$$B(t)=\int_0^t b(t)\beta(t-a)K(a,t,P)B(a)\,da+\int_0^\infty b(t)\beta(a+t)\phi(a)M(a,t,P)\,da,$$

$$P(t)=\int_0^t K(a,t,P)B(a)\,da+\int_0^\infty \phi(a)M(a,t,P)\,da. \tag{14}$$

The process described above shows that if ρ is a solution of equations (1)–(3), then B and P satisfy the coupled integral equations (14). Conversely, if B and P are nonnegative continuous solutions of equations (14), then by equations (8), ρ is the solution of equations (1)–(3). Hence, we note the equivalence between the partial differential equations (1)–(3) and the integral equations (14) in the sense that existence and uniqueness of equations (1)–(3) can be obtained in terms of those of equations (14).

Theorem 2.1

Let ρ be a solution of equations (1)–(3) on $[0, T]$. Then the total population P and the birth rate B satisfy the integral equations (14). Conversely, if P and B are nonnegative continuous solutions of equations (14), then the function defined by equations (8) on $\mathbb{R}^+ \times [0, T]$ is a solution of (1.1)–(1.3).

For fixed $P \in C^+[0, T]$, equation $(2.7)_1$ is a linear Volterra integral equation for B. Hence, it has a unique solution on $[0, T]$, which is denoted by

$$B(t)=\mathscr{B}_T(P)(t). \tag{15}$$

Using this solution, we define an operator $\mathscr{P}_T$ on $C^+[0, T]$ by

$$\mathscr{P}_T(P)(t)=\int_0^T K(a,t,P)\mathscr{B}_T(P)(a)\,da+\int_0^\infty \phi(a)M(a,t,P)\,da. \tag{16}$$

Obviously,

$$\mathscr{B}_T,\ \mathscr{P}_T\colon C^+[0,T]\to C^+[0,T].$$

Then, to prove existence and uniqueness of solutions of equations (1)–(3) on $\mathbb{R}^+ \times [0, T]$, it is sufficient to show the existence and uniqueness of a fixed point of the operator $\mathscr{P}_T$.

Let

$$\Phi=\int_0^\infty \phi(a)\,da \quad \text{and} \quad R_T=\{g \mid g \in C^+[0,T], \|g-\Phi\|_T \leqslant d\},$$

where $\|\cdot\|_T$ is a supremum norm in $C^+[0, T]$ and $d > 0$ is a constant.

First, we show that $\mathscr{P}_T(P)$ maps R_T into itself.
From the assumptions,

$$\mathscr{B}_T(P)(t) = \int_0^t b(t)\beta(t-a)K(a,t,P)\mathscr{B}_T(P)(a)\,da + \int_0^\infty b(t)\beta(a+t)\phi(a)M(a,t,P)\,da \leqslant b^*\bar{\beta}\int_0^t \mathscr{B}_T(P)(a)\,da + b^*\bar{\beta}\bar{\Phi}.$$

By Gronwall's inequality,

$$\mathscr{B}_T(P)(t) \leqslant b^*\bar{\beta}\Phi \exp(b^*\bar{\beta}t). \tag{17}$$

Hence,

$$|\mathscr{P}_T(P)(t) - \Phi| \leqslant b^*\bar{\beta}\Phi\int_0^t \exp(b^*\bar{\beta}a)\,da + \int_0^\infty \phi(a)|M(a,t,P)-1|\,da$$
$$\leqslant \Phi[\exp(b^*\bar{\beta}T)-1] + \Phi(\bar{c}+\bar{\mu}+\bar{f})T[\exp(\bar{c}+\bar{\mu}+\bar{f})T]$$

since

$$|M(a,t,P)-1| = \left|\exp\left[-\int_0^t (c(\tau)+\mu(a+\tau)+f(P(\tau)))\,d\tau\right]-1\right|$$
$$\leqslant \left|\int_0^t (c(\tau)+\mu(a+\tau)+f(P(\tau))\,d\tau\right|$$
$$\times \exp\left[\int_0^t |c(\tau)+\mu(a+\tau)+f(P(\tau)))|\,d\tau\right]$$
$$\leqslant (\bar{c}+\bar{\mu}+\bar{f})T\exp[(\bar{c}+\bar{\mu}+\bar{f})T]$$

for $0 \leqslant t \leqslant T$. It follows that $\mathscr{P}_T(P) \in R_T$ for T small.

As the next step, if we can show that $\mathscr{P}_T(P)$ is attractive, then by the contraction mapping principle, $\mathscr{P}_T(P)$ has a unique fixed point.

$$\|\mathscr{P}_T(P) - \mathscr{P}_T(Q)\| \leqslant \int_0^t |K(a,t,P)-K(a,t,Q)|\mathscr{B}_T(P)(a)\,da + \int_0^t K(a,t,Q)|\mathscr{B}_T(P)(a)-\mathscr{B}_T(Q)(a)|\,da + \int_0^t |M(a,t,P)-M(a,t,Q)|\phi(a)\,da. \tag{18}$$

We, then, estimate the three parts on the right of inequality (18).

$$|K(a,t,P)-K(a,t,Q)| = \exp\left[-\int_0^{t-a}(c(a+\tau)+\mu(\tau))\,d\tau\right] \times \left|\exp\left[-\int_0^{t-a} f(P(a+\tau))\,d\tau\right] - \exp\left[-\int_0^{t-a} f(Q(a+\tau))\,d\tau\right]\right|$$
$$\leqslant \left|1-\exp\left[\int_0^{t-a}(f(P(a+\tau))-f(Q(a+\tau)))\,d\tau\right]\right| \leqslant kT\exp(2\bar{f}T)\|P-Q\|_T \tag{19}$$

where $k = \sup f'(P)$. Similarly,

$$|M(a,t,P)-M(a,t,Q)| \leqslant kT\exp(2\bar{f}T)\|P-Q\|_T. \tag{20}$$

Let $\eta(t) = \mathscr{B}_T(P)(t) - \mathscr{B}_T(Q)(t)$.

$$\eta(t) = \int_0^t b(t)\beta(t-a)K(a,t,P)\eta(a)\,da + \int_0^t b(t)\beta(t-a)(K(a,t,P)-K(a,t,Q))\mathscr{B}_T(Q)(a)\,da + \int_0^\infty b(t)\beta(a+t)\phi(a)(M(a,t,P)-M(a,t,Q))\,da.$$

Via inequalities (17) and (19),

$$\left|\int_0^t b(t)\beta(t-a)(K(a,t,P)-K(a,t,Q))\mathscr{B}_T(Q)(a)\,da\right| \leqslant C_1\|P-Q\|_T,$$

$$\left|\int_0^\infty b(t)\beta(a+t)\phi(a)(M(a,t,P)-M(a,t,Q))\,da\right| \leqslant C_2\|P-Q\|_T.$$

Thus,

$$|\eta(t)| \leqslant \tilde{C}\|P-Q\|_T + b^*\bar{\beta}\int_0^t \eta(a)\,da$$

and by Gronwall's inequality again,

$$\|\eta(t)\| \leqslant \tilde{C}\exp(b^*\bar{\beta}T)\|P-Q\|_T. \tag{21}$$

Substituting inequalities (19)–(21) into (18),

$$\|\mathscr{P}_T(P)-\mathscr{P}_T(Q)\| \leqslant \bar{k}\|P-Q\|_T, \tag{22}$$

where $\bar{k}<1$ for T small. This shows that there exists a $T>0$ such that the operator $\mathscr{P}_T$: $C^+[0,T]\to C^+[0,T]$ defined by equation (16) has a unique fixed point and, hence, gives local existence and uniqueness. We can also easily get global existence and uniqueness. In fact, as it is shown above, the time T is a continuous function of Φ, which is the initial population size at time 0. On the other hand, from equation (7), $\rho(a,t)$ is continuous as long as it exists and so is $P(t)$. Hence, $P(t)$ is bounded on $[0,T]$. Using $P(T)$ as an initial size at time T and following the same procedure as above, we can get another time interval $[T,T_1]$ on which the solution exists and is unique and continuous. Continuing in this process, we get existence and uniqueness on $[T,T_\infty)$. Now we claim $T_\infty=\infty$. From equation $(14)_1$,

$$B(t) \leqslant b^*\bar{\beta}\int_0^t B(a)\,da + b^*\bar{\beta}\Phi.$$

By virtue of Gronwall's inequality,

$$B(t) \leqslant b^*\bar{\beta}\Phi\exp(b^*\bar{\beta}t). \tag{23}$$

Substituting inequality (23) into equation $(14)_2$,

$$P(t) \leqslant b^*\bar{\beta}\Phi\int_0^t \exp(b^*\bar{\beta}\tau)\,d\tau + \Phi = \exp(b^*\bar{\beta}t). \tag{24}$$

If $T_\infty<\infty$, then $\rho(a,t)$ has to be unbounded as $t\to T_\infty$. By viewing expression (24), clearly, it is impossible. Therefore, $T_\infty=\infty$. This gives global existence and uniqueness. Hence we have Theorem 2.2.

Theorem 2.2

Under the hypotheses (5)–(7), the system (1)–(3) has a unique solution defined on $[0,\infty)$.

3. SURVIVAL OF POPULATIONS AS SOLUTIONS OF THE EQUATION

In this section, we investigate persistence and extinction of populations modelled by the system (1)–(3). Persistence and extinction of populations relate to the positivity of the total population size

$$P(t) = \int_0^\infty \rho(a, t)\, da.$$

There does not exist any finite time t such that $P(t) = 0$ because this leads to $\rho(a, t) \equiv 0$, which is not a solution of the system (1)–(3). On the other hand, no individuals will survive beyond some maximum age. Hence,

$$\lim_{t\to\infty} P(t) = 0 \quad \text{if and only if} \quad \lim_{t\to\infty} \rho(a, t) = 0, \quad \text{for all } a.$$

This motivates the following definition of persistence.

Definition 3.1

(1) A population, represented by a solution $\rho(a, t)$ of system (1)–(3) is *persistent* if

$$\liminf_{t\to\infty} \rho(a, t) > 0;$$

(2) A population goes to *extinction* if $\lim_{t\to\infty} \rho(a, t) = 0$.

We have shown the global existence and uniqueness of the system (1)–(3) in the previous section. Thus, the following change of variables is well defined:

$$m(a, t) = \exp\left[\int_0^t (c(\tau) + f(P(\tau)))\, d\tau\right] \rho(a, t). \tag{25}$$

Now, we make this change of variables to simplify the system.

$$\frac{\partial m(a, t)}{\partial a} = \exp\left[\int_0^t (c(\tau) + f(P(\tau)))\, d\tau\right] \frac{\partial \rho(a, t)}{\partial a}, \tag{26}$$

$$\frac{\partial m(a, t)}{\partial t} = (c(t) + f(P(t)))\exp\left[\int_0^t (c(\tau) + f(P(\tau)))\, d\tau\right] \rho(a, t)$$

$$+ \exp\left[\int_0^t (c(\tau) + f(P(\tau)))\, d\tau\right] \frac{\partial \rho(a, t)}{\partial t}. \tag{27}$$

Hence,

$$\frac{\partial m(a, t)}{\partial a} + \frac{\partial m(a, t)}{\partial t} = -\mu(a)\exp\left[\int_0^t (c(\tau) + f(P(\tau)))\, d\tau\right] \rho(a, t)$$

$$= -\mu(a) m(a, t).$$

The renewal equation becomes

$$m(0, t) = \exp\left[\int_0^t (c(\tau) + f(P(\tau)))\, d\tau\right] \rho(0, t) = \int_0^\infty b(t)\beta(a) m(a, t)\, da.$$

Obviously,

$$m(a, 0) = \rho(a, 0).$$

Collecting these changes, we arrive at a new system

$$\frac{\partial m(a, t)}{\partial a} + \frac{\partial m(a, t)}{\partial t} = -\mu(a) m(a, t),$$

$$m(0,t)=\int_0^t b(t)\beta(a)m(a,t)\,\mathrm{d}a, \tag{28}$$
$$m(a,0)=\phi(a).$$

Time variation and density dependence no longer appear in the mortality function. This simplifies the analysis and stable age distribution theory can be applied, as will be seen later.

Although the fertility function still involves time variation it is bounded by the assumption $b_* \leqslant b(t) \leqslant b^*$. This provides motivation to consider a comparison technique.

We need the following lemmas.

Lemma 3.1 [26]

Let $f(x) \in L_2[a,b]$ and $N(x,y)$ be continuous for $x, y \in [a,b]$. Then the equation

$$u(x)=f(x)+\lambda\int_a^x N(x,y)u(y)\,\mathrm{d}y$$

has a unique bounded solution, given by

$$u(x)=f(x)+\lambda\int_a^x \Gamma(x,y,\lambda)f(y)\,\mathrm{d}y,$$

where the resolvent kernel

$$\Gamma(x,y,\lambda)=\sum\lambda^n N_{n+1}(x,y)$$

and the iterated kernel

$$N_{n+1}(x,y)=\int_y^x N(x,z)N_n(z,y)\,\mathrm{d}z,$$

where $N_1(x,y)=N(x,y)$.

Using Lemma 3.1, the following is a straightforward result.

Lemma 3.2

Assume

$$f_i(x)\geqslant 0,\quad N_i(x,y)\geqslant 0,\quad i=1,2,\quad \forall x, y\in[a,b].$$

Let $u_i(x)$ be solutions of

$$u_i(x)=f_i(x)+\int_a^x N_i(x,y)u_i(y)\,\mathrm{d}y,\quad i=1,2,$$

respectively. Then

$$u_1(x)\leqslant u_2(x),$$

if either

$$f_1(x)\leqslant f_2(x)\quad\text{and}\quad N_1(x,y)\equiv N_2(x,y),$$

or

$$f_1(x)\equiv f_2(x)\quad\text{and}\quad N_1(x,y)\leqslant N_2(x,y).$$

To set up appropriate boundary conditions for the population model, the next lemma is useful.

Lemma 3.3

Let $\beta(a)$ and $u(a)$ be nonnegative continuous functions satisfying

$$u(0)=\lambda\int_0^\infty \beta(a)u(a)\,\mathrm{d}a$$

where $\lambda > 0$. Then, for any $\theta \geqslant \lambda$, there exists a continuous function $v(a)$ such that

$$v(0) = \theta \int_0^\infty \beta(a)v(a)\,da$$

and

$$v(a) \geqslant u(a), \quad \forall a \geqslant 0.$$

Proof. Let

$$v(a) = u(a) + C\exp(\delta a), \tag{29}$$

where $C > 0$ and δ are to be determined. Then,

$$v(0) = u(0) + C = \lambda \int_0^\infty \beta(a)u(a)\,da + C.$$

To satisfy

$$\begin{aligned} v(0) &= \theta \int_0^\infty \beta(a)v(a)\,da \\ &= \theta \int_0^\infty \beta(a)u(a)\,da + C\theta \int_0^\infty \beta(a)\exp(\delta a)\,da \end{aligned}$$

we need

$$C - (\theta - \lambda)\int_0^\infty \beta(a)u(a)\,da = C\theta \int_0^\infty \beta(a)\exp(\delta a)\,da. \tag{30}$$

Denote

$$(\theta - \lambda)\int_0^\infty \beta(a)u(a)\,da = W.$$

Then

$$C - W = C\theta \int_0^\infty \beta(a)\exp(\delta a)\,da;$$

i.e.

$$C = \frac{W}{1 - \theta \int_0^\infty \beta(a)\exp(\delta a)\,da}. \tag{31}$$

By choosing a proper δ, C is positive. This gives desirable $v(a)$.

Consider two comparison systems:

$$\begin{aligned} &\frac{\partial m^*(a,t)}{\partial a} + \frac{\partial m^*(a,t)}{\partial t} = -\mu(a)m^*(a,t), \\ &m^*(0,t) = b^* \int_0^\infty \beta(a)m^*(a,t)\,da, \\ &m^*(a,0) = \phi^*(a), \end{aligned} \tag{32}$$

where $\phi^*(a)$ is an arbitrary continuous function satisfying $\phi(a) \leqslant \phi^*(a)$, $\forall a \geqslant 0$, and

$$\phi^*(0) = b^* \int_0^\infty \beta(a)\phi^*(a)\,da.$$

$$\frac{\partial m_*(a,t)}{\partial a} + \frac{\partial m_*(a,t)}{\partial t} = -\mu(a)m_*(a,t),$$

$$m_*(0,t) = b_* \int_0^\infty \beta(a) m_*(a,t)\,da \tag{33}$$
$$m_*(a,0) = \phi_*(a)$$

where $\phi_*(a)$ is an arbitrary continuous function satisfying $\phi_*(a) \leqslant \phi(a)$, $\forall a \geqslant 0$, and

$$\phi_*(0) = b_* \int_0^\infty \beta(a)\phi_*(a)\,da.$$

By Lemma 3.3, $\phi^*(a)$ and $\phi_*(a)$ exist.

Theorem 3.1

Let $m(a,t)$, $m^*(a,t)$ and $m_*(a,t)$ be solutions of systems (28), (32) and (33), respectively. Then

$$m_*(a,t) \leqslant m(a,t) \leqslant m^*(a,t) \tag{34}$$

for all $a \geqslant 0$, $t \geqslant 0$.

Proof. Along characteristics,

$$m_*(a,t) = \begin{cases} B_*(t-a)\exp\left[-\int_0^a \mu(\tau)\,d\tau\right], & a \leqslant t \\ \phi_*(a-t)\exp\left[-\int_0^t \mu(a-t+\tau)\,d\tau\right], & a \geqslant t \end{cases} \tag{35}$$

where

$$B_*(t) = m_*(0,t)$$
$$= \int_0^\infty b_*\phi_*(a)\beta(a+t)\hat{M}(a,t)\,da + \int_0^t b_*\beta(t-a)\hat{K}(a,t)B_*(a)\,da; \tag{36}$$

$$m(a,t) = \begin{cases} B(t-a)\exp\left[-\int_0^a \mu(\tau)\,d\tau\right], & a \leqslant t \\ \phi(a-t)\exp\left[-\int_0^t \mu(a-t+\tau)\,d\tau\right], & a \geqslant t \end{cases} \tag{37}$$

where

$$B(t) = m(0,t)$$
$$= \int_0^\infty b(t)\phi(a)\beta(a+t)\hat{M}(a,t)\,da + \int_0^t b(t)\beta(t-a)\hat{K}(a,t)B(a)\,da; \tag{38}$$

and

$$m^*(a,t) = \begin{cases} B^*(t-a)\exp\left[-\int_0^a \mu(\tau)\,d\tau\right], & a \leqslant t \\ \phi^*(a-t)\exp\left[-\int_0^t \mu(a-t+\tau)\,d\tau\right], & a \geqslant t \end{cases} \tag{39}$$

where

$$B^*(t) = m^*(0,t)$$
$$= \int_0^\infty b^*\phi^*(a)\beta(a+t)\hat{M}(a,t)\,da + \int_0^t b^*\beta(t-a)\hat{K}(a,t)B^*(a)\,da. \tag{40}$$

Here

$$\begin{cases} \hat{K}(a,t) = \exp\left[-\int_0^{t-a} \mu(\tau)\,d\tau\right] \\ \hat{M}(a,t) = \exp\left[-\int_0^{t} \mu(a+\tau)\,d\tau\right] \end{cases} \tag{41}$$

By Lemma 3.3,

$$B_*(t) \leqslant B(t) \leqslant B^*(t)$$

and from the expressions (35), (37) and (39), the proof is completed.

Now, we focus on the system (32) and observe the following. By a well known result [27] the system (32) has a separable solution

$$m^*(a,t) = A(a)T(t)$$

if and only if the equation

$$b^* \int_0^\infty \beta(a)\exp(-ra)\exp\left[-\int_0^a \mu(s)\,ds\right]da = 1 \tag{42}$$

has a real solution $r = r^*$ in which case the solution has the form

$$m^*(a,t) = C^* \exp\left[r^*(t-a)\right]\exp\left[-\int_0^a \mu(s)\,ds\right],$$

where C^* is a positive constant.

Define

$$R^*(r) = b^* \int_0^\infty \beta(a)\exp(-ra)\exp\left[-\int_0^a \mu(s)\,ds\right]da.$$

Since $\beta(a)$ has compact support on $[0, \infty)$,

$$\lim_{r\to-\infty} R^*(r) = +\infty,$$

$$\lim_{r\to+\infty} R^*(r) = 0.$$

Notice that

$$R'^*(r) = -b^* \int_0^\infty a\beta(a)\exp(-ra)\exp\left[-\int_0^a \mu(s)\,ds\right]da < 0.$$

It follows that the equation (42) has a unique real solution r^*. We can analogously discuss the system (33). With these lemmas the following main result can be obtained.

Theorem 3.2

The population, described by the system (1)–(3), is persistent if

$$\int_0^\infty (r_* - c(\tau))\,d\tau > -\infty, \tag{43}$$

where r_* is the real solution of

$$\int_0^\infty \beta(a)\exp(-ra)\exp\left[-\int_0^a \mu(s)\,ds\right]da = \frac{1}{b_*}; \tag{44}$$

the population goes to extinction if

$$\int_0^\infty (r^* - c(\tau))\,d\tau = -\infty, \tag{45}$$

where r^* is the real solution of

$$\int_0^\infty \beta(a)\exp(-ra)\exp\left[-\int_0^a \mu(s)\,ds\right]da = \frac{1}{b_*}. \tag{46}$$

Proof. As we discussed above,

$$m^*(a,t) = C^*\exp(r^*t)\exp\left[-\left(r^*a + \int_0^a \mu(s)\,ds\right)\right] \equiv \exp(r^*t)E^*(a)$$

and

$$m_*(a,t) = C_*\exp(r_*t)\exp\left[-\left(r_*a + \int_0^a \mu(s)\,ds\right)\right] \equiv \exp(r_*t)E_*(a).$$

By Theorem 3.1,

$$E_*(a)\exp(r_*t) \leqslant m(a,t) \leqslant E^*(a)\exp(r^*t). \tag{47}$$

Hence

$$E_*(a)\exp\left[\int_0^t (r_* - c(\tau))\,d\tau\right]\exp\left[-\int_0^t f(P(\tau))\,d\tau\right] \leqslant \rho(a,t)$$

$$\leqslant E^*(a)\exp\left[\int_0^t (r^* - c(\tau))\,d\tau\right]\exp\left[-\int_0^t f(P(\tau))\,d\tau\right]. \tag{48}$$

Let the hypothesis (43) hold and let

$$\int_0^\infty (r_* - c(\tau))\,d\tau \geqslant -H > -\infty.$$

Then

$$\rho(a,t) \geqslant E_*(a)\exp\left[\int_0^t (r_* - c(r))\,d\tau\right]\exp\left[-\int_0^t f(P(\tau))\,d\tau\right]$$

$$\geqslant E_*(a)\exp(-H)\exp\left[-\int_0^t f(P(\tau))\,d\tau\right]. \tag{49}$$

Suppose that the population goes to extinction. Then $P(t)\to 0$, as $t\to\infty$ and there exists a positive number δ such that $P(t) \leqslant \delta < \infty$, $\forall t \geqslant 0$. Since $f(0) = 0$ and $f(P)$ is increasing and nonnegative,

$$\int_0^t f(P(\tau))\,d\tau \leqslant \int_0^\delta f(y)\,dy \equiv \hat{N}.$$

It follows that

$$\rho(a,t) \geqslant E_*(a)\exp[-(H+\hat{N})] > 0$$

uniformly for all $t \leqslant 0$, a contradiction. This completes the first part of the proof.

Next, it is clear that

$$\rho(a,t) \leqslant E^*(a)\exp\left[\int_0^t (r^* - c(\tau))\,d\tau\right]\exp\left[-\int_0^t f(P(\tau))\,d\tau\right]$$

$$\leqslant E^*(a)\exp\left[\int_0^t (r^* - c(\tau))\,d\tau\right] \to 0, \quad \text{as } t\to\infty$$

if the hypothesis (45) is satisfied. This completes the proof.

Corollary 3.1

Assume

$$\int_0^\infty c(t)\,dt < \infty.$$

Then, the population is persistent if

$$\int_0^\infty \beta(a)\exp\left[-\int_0^a \mu(s)\,ds\right]da \geqslant \frac{1}{b_*} \tag{50}$$

and the population goes to extinction if

$$\int_0^\infty \beta(a)\exp\left[-\int_0^a \mu(s)\,ds\right]da < \frac{1}{b^*}. \tag{51}$$

If

$$\int_0^\infty c(t)\,dt = \infty$$

then the population goes to extinction provided

$$\int_0^\infty \beta(a)\exp\left[-\int_0^a \mu(s)\,ds\right]da \leqslant \frac{1}{b^*}. \tag{52}$$

Proof. Suppose

$$\int_0^\infty c(t)\,dt < \infty.$$

From inequality (50), it follows that $r_* \geqslant 0$ which leads to expression (43). Consequently, the population is persistent. From expression (51) it follows $r^* < 0$ and equation (45) holds; this leads to the conclusion that the population goes to extinction.

When

$$\int_0^\infty c(t)\,dt = \infty,$$

inequality (52) implies $r^* \leqslant 0$ and, consequently, that equation (45) holds. This gives extinction for the population.

Remark 3.1

If the mortality is time independent, $c(t) = 0$. Then, inequality (50) leads to persistence and expression (51) gives extinction for the population.

The following is a direct consequence of Theorem 3.2.

Corollary 3.2

Assume that the fertility is time independent; that is, $b(t) \equiv b = \text{constant}$. Then the population goes to extinction if and only if

$$\int_0^\infty (\tau - c(\tau))\,d\tau = -\infty,$$

where r is the real solution of the equation

$$b\int_0^\infty \beta(a)\exp(-ra)\exp\left[-\int_0^a \mu(s)\,ds\right]da = 1.$$

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